STUDIES IN NEOTROPICAL PALEOBOTANY. III. THE TERTIARY COMMUNITIES OF PANAMA – GEOLOGY OF THE POLLEN-BEARING DEPOSITS¹

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ABSTRACT

Samples containing fossil pollen and spores were collected from six sites representing five Tertiary formations in Panama. The Gatuncillo Formation is middle(?) to late Eocene, based on foraminifera and mollusk fossils. The formation is exposed around Madden Basin and samples were collected in the vicinity of Alcalde Díaz (Peñoncito). Material from the early Miocene Culebra Formation was obtained from a well drilled in the Contractor's Hill locality at the base of Gold Hill. The Cucaracha Formation overlies the Culebra and is also early Miocene in age. The Cucaracha material was collected from exposures along the Gaillard Cut section of the Canal. The early Miocene La Boca Formation outcrops in the same area. Although these three formations are similar in age (early Miocene), field evidence demonstrates that they are sequential from the Culebra (oldest), through the Cucaracha, to the La Boca (youngest). The Gatun Formation is late Miocene and early Pliocene in age and core samples were taken from a series of wells drilled in Gatun Lake. The location, stratigraphy, lithology, and depositional environments are summarized for these five formations. In subsequent publications the paleocommunities, paleoenvironments, and biogeographic implications will be considered for each of the microfloras.

The present studies on the Cenozoic history of neotropical vegetation began in 1964 with a collection of pollen-bearing samples from Tertiary deposits in central Panama. Subsequently, other samples were obtained from the Oligocene of Puerto Rico and the Miocene of Veracruz, Mexico. At that time the vegetation of Central America was poorly known, but research by staff of the Missouri Botanical Garden, the Field Museum, and various institutions in Central America was rapidly providing new information on the composition of the flora, and on the range, ecology, and biogeographic relationships of its components. By comparison, the vegetation of more restricted areas to the north, such as Puerto Rico and Veracruz, was somewhat better known (Howard, 1973; Gomez-Pompa, 1973), and it seemed logical to begin paleofloristic studies on geologically younger deposits in these areas where modern analogs were more clearly defined. Consequently, our first studies were on the middle Oligocene San Sebastian palynoflora from Puerto Rico (Graham & Jarzen, 1969), followed by the late Miocene Paraje Solo palynoflora from Veracruz, Mexico (Graham, 1976).

The older Gatuncillo assemblage from Panama proved the most difficult of our neotropical studies, and recently accumulated information on the modern vegetation was most helpful in making paleoenvironmental reconstructions. The completion of the "Flora of Panama" (1980) and Croat's (1978) "Flora of Barro Colorado Island," initiation of Burger's "Flora Costaricensis," and the "Flora Mesoamerica," coordinated through the Missouri Botanical Garden and Kew, are making both specimens and information available to our studies on vegetational history. Recent biogeographic summaries are also valuable for interpreting the paleofloristic data (e.g., Gentry, 1982). Also, the pollen and spore reference collection, used for identification of the fossil palynomorphs, has increased from 10,000 slides in 1964 to nearly 22,000. From the standpoint of geology, the recently revised "Geologic Map of the Panama Canal and Vicinity, Republic of Panama" (Stewart et al., 1980) and modern plate tectonic summaries (e.g., Coney, 1982; Raven & Axelrod, 1974) are important for placing the paleobotanical data in a sound geologic context.

The decision to defer consideration of the Panama material was fortunate for several reasons. Pollen-bearing samples from five Tertiary formations were collected in Panama within or adjacent to the former Canal Zone (Figs. 1–3). These

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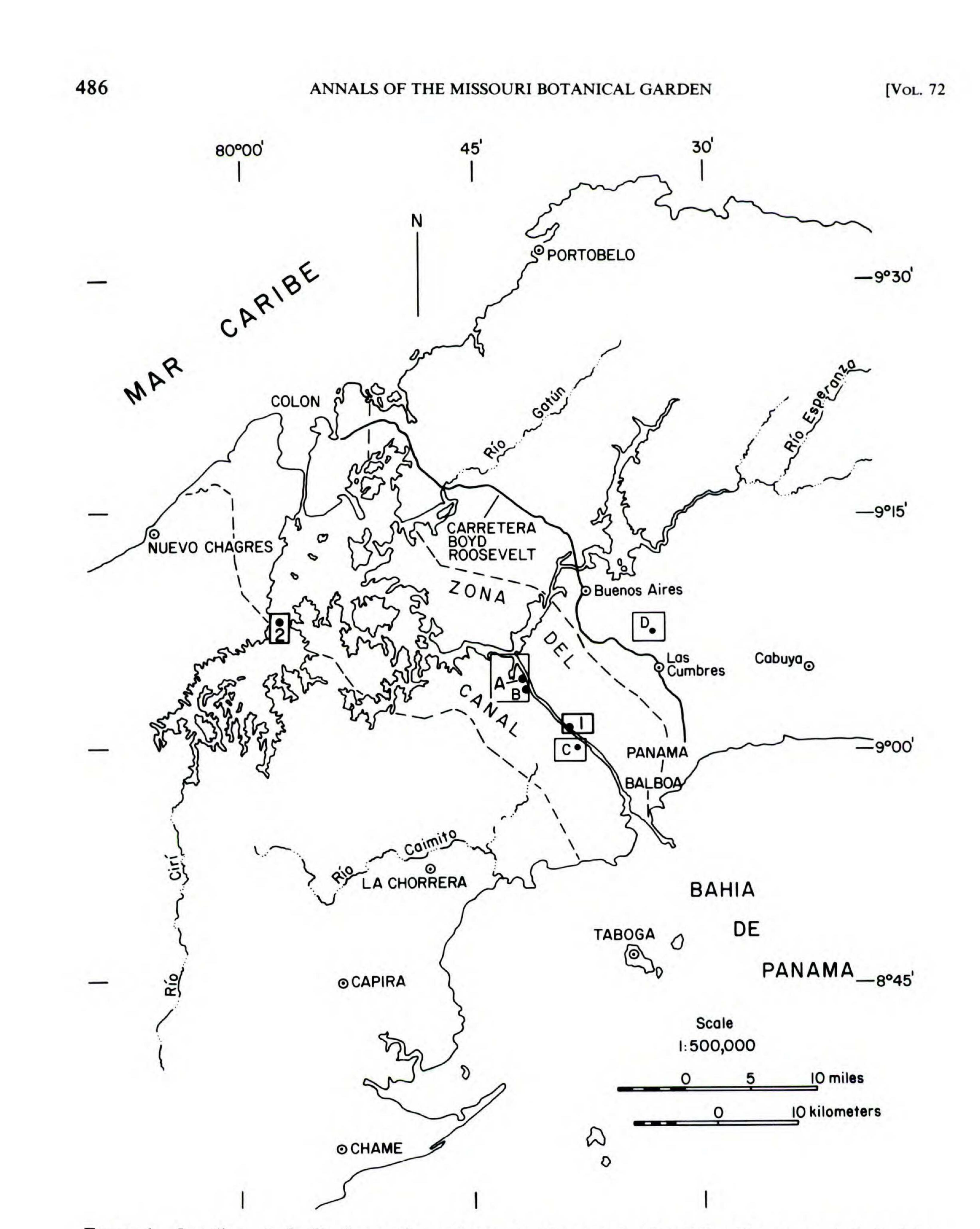


FIGURE 1. Locality map for Tertiary pollen and spore-bearing samples, Republic of Panama. – A, B. La Boca Formation (early Miocene), Las Cascadas Reach of Gaillard Cut, Panama Canal. – C. Cucaracha Formation (early Miocene), Culebra-Cucaracha Reach. – D. Gatuncillo Formation [Middle(?) to late Eocene], near Alcalde Díaz (Peñoncito). – 1. Drilling site through the Culebra Formation (early Miocene), Contractor's Hill locality in front of Gold Hill (core GH-9). – 2. Drilling site through the Gatun Formation (late Miocene to Pliocene), Gatun Lake (cores SL-48, 49, 60, 103).

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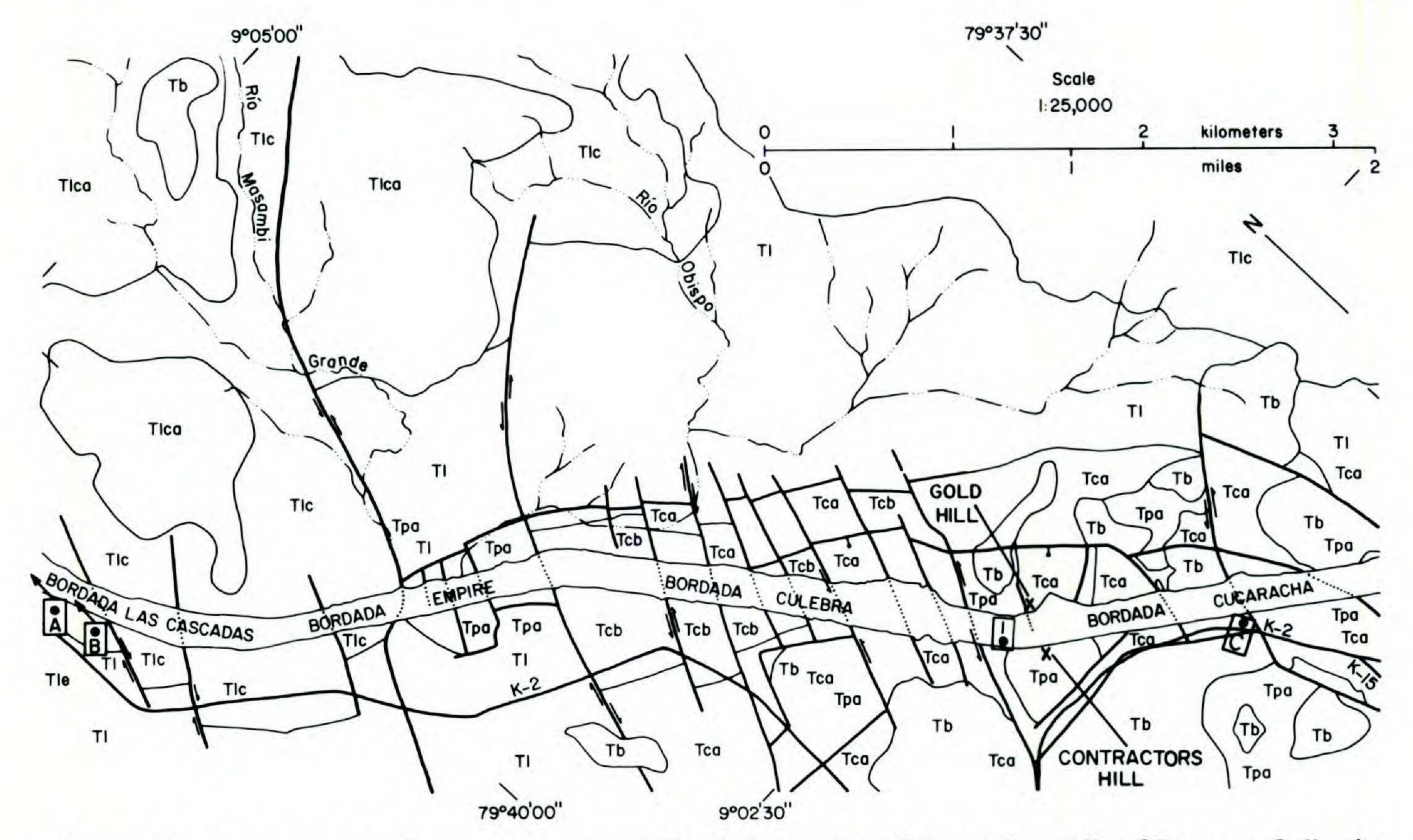


FIGURE 2. Generalized surface geology map, Gaillard Cut section of Canal, Republic of Panama. Collecting sites A and B (La Boca Formation) are along a Canal-facing slope overlain by the Las Cascadas Formation (Tlc), and C (Cucaracha Formation) is overlain in part by the Pedro Miguel Formation (Tpa). Note extensive faulting. Modified from Stewart et al. (1980). Symbols: Tlc-Las Cascadas Formation; Tl-La Boca; Tle-Emperador Limestone member (coralliferous limestone) of La Boca Formation; Tpa-Pedro Miguel; Tcb-Culebra; Tca-Cucaracha; Tlca-andesite, equal in age to Las Cascadas Formation (early Miocene); Tb-intrusive and extrusive

basalts (middle and late Miocene).

are the middle(?) to late Eocene Gatuncillo Formation, the early Miocene Culebra, Cucaracha, and La Boca Formations, and the late Miocene to Pliocene Gatun Formation.

The instability of the landscape along the Gaillard Cut, as reflected by the faults shown in Figure 2, presents problems in recognizing the age and stratigraphic relations between the numerous, small, segmented outcrops that are frequently concealed by dense vegetation cover. In addition, special problems arise from maintenance procedures used along the Canal, which often involve removal of vast amounts of slope sediments (Figs. 9-11). This significantly alters the landscape, even between collecting seasons. These procedures are required by the unusual geologic configuration through which the Canal was constructed. During the Tertiary, lava filled many of the valleys and river basins. Subsequent erosion of the softer surrounding sediments below the basalt-filled basins produced a present-day inverted topography in which the modern hills were originally topographic lows. The result is massive, dense basalts resting on top of softer underlying sediments. When the Canal was dug through this mosaic, the weight of the overlying basalts began forcing enormous volumes of sediment into the Canal. The scars from these slippages are a common and characteristic feature of the banks along the Canal. To reduce landslides, the slope face is cut back, and these alterations, combined with the landslides, considerably complicate permanently recording the location and determining the stratigraphic relationships between many of the collecting sites.

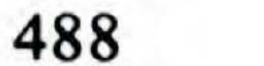
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The present paper summarizes the geology, depositional environments, and currently accepted ages for five Tertiary formations in Panama from

which pollen-bearing samples have been collected. Subsequent studies will trace the history of the vegetation in central Panama as preserved in the palynofloras of the Gatuncillo, Culebra, Cucaracha, La Boca, and Gatun Formations.

THE GATUNCILLO FORMATION

The Gatuncillo Formation was named by Thompson in Panama Canal reports for 1944



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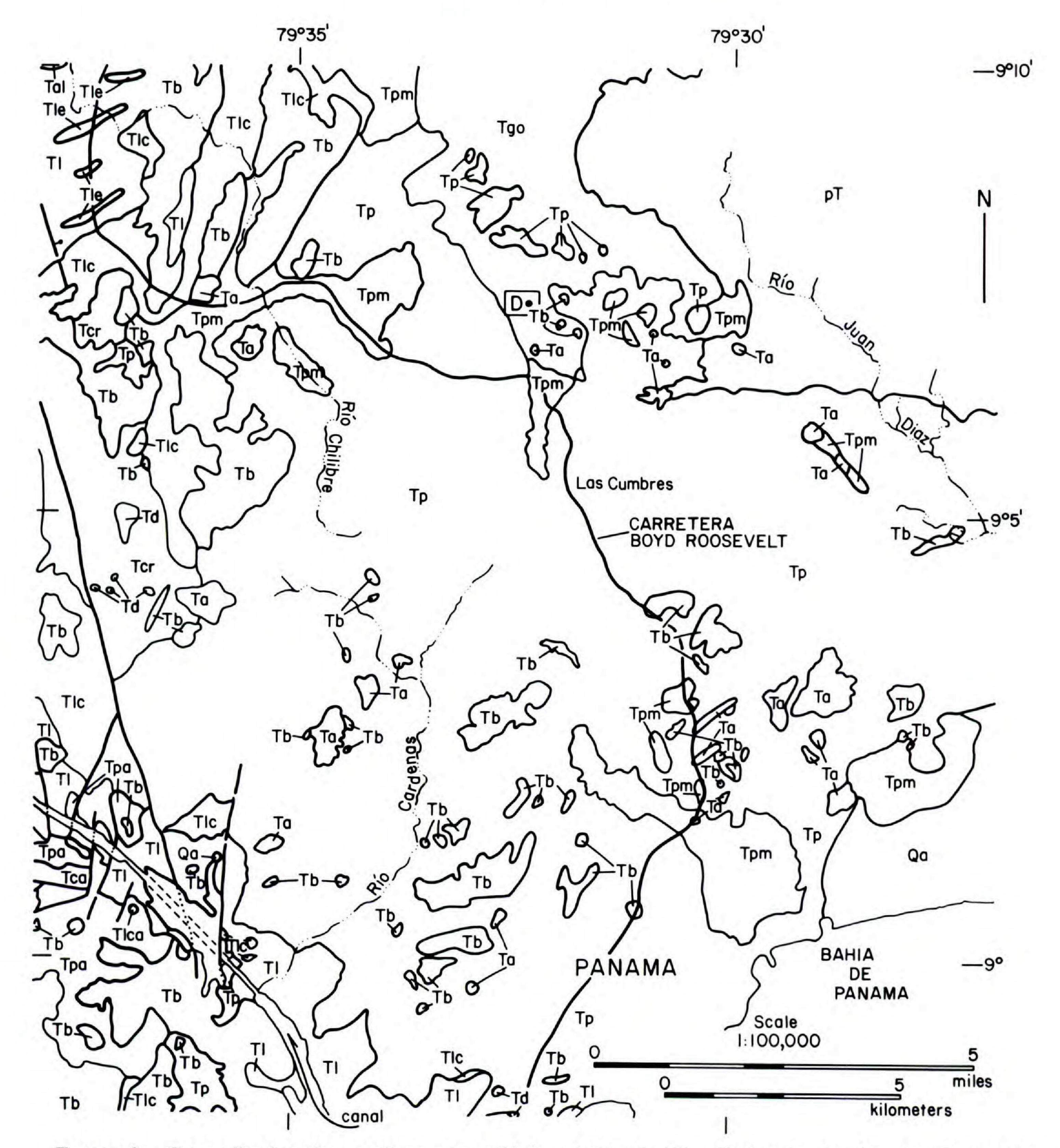


FIGURE 3. Generalized surface geology map, vicinity of Alcalde Díaz [Peñoncito; locality D-Gatuncillo Formation, middle(?) to late Eocene]. Symbols: Tp-Panama Formation (early to late Oligocene); Tpm-Panama (marine facies); Tgo-Gatuncillo; Ta-intrusive and extrusive andesite (Oligocene and early Miocene); Td-intrusive dacite and dacite porphyry (Miocene); Tcr-Caraba (late Oligocene); Qa-Holocene (alluvium or fill). For other symbols see legend to Figure 2.

and first published in Woodring and Thompson (1949). Maximum thickness is about 1,000 m and the formation "unconformably overlies a basement complex of unknown, possibly Cretaceous age consisting of strongly deformed altered volcanics-flows, pyroclastics, and indurated fine-grained sediments that probably were

originally fine-grained tuffs" (Woodring & Thompson, 1949: 227).

In the vicinity of our collection sites the formation outcrops around the margins of Madden Basin and Lake Madden north of Panama City (Fig. 3). The Rio Gatun fault terminates the exposure to the north, and the Azota fault defines

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portions of its western limits. A few isolated outcrops occur to the west along Gatun Lake and at the north end of Culebra Reach. Elsewhere the formation has been identified in cores to the south as far as Gold Hill and north of Gamboa. In addition, it has been recognized eastward into the Bayano River basin and westward as far as the Costa Rica-Panama border. There are also massive outcrops in the southern part of the Azuero Peninsula.

occur in the middle Eocene, and two of these (Yaberinella jamaicensis and Fabiania cubensis) are known only from the middle Eocene. Consequently, Cole (1952) refers the Gatuncillo Formation to the middle(?) and late Eocene.

Samples for pollen and spore analysis were obtained from a roadcut section near Alcalde Díaz just off the Boyd-Roosevelt highway (our locality D, Figs. 1, 3-5; samples 1-15; 9°7'N, 79°32'W). The concurrence of the mollusk and foraminifera data, in the absence of any conflicting stratigraphic information, indicates the palynomorphs recovered from the Gatuncillo Formation represent remnants of a middle to late Eocene plant community growing in the region approximately 40 Ma.

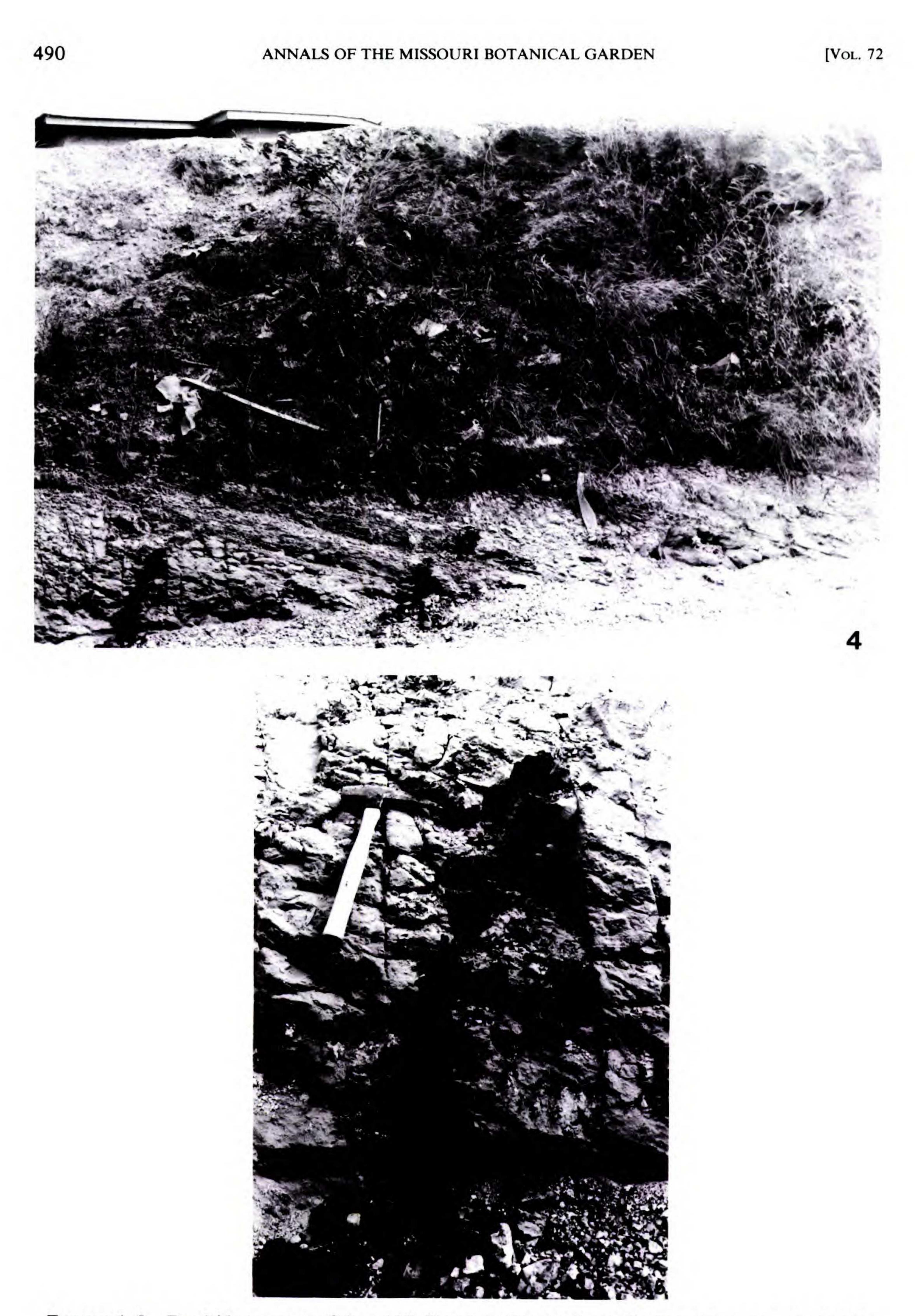
Local extrusive basalts of Miocene age overlie small areas of the Gatuncillo Formation, and just north of Alcalde Díaz (Peñoncito) there are very local deposits of the Panama Formation forming the tops of hills. The latter is early to late Oligocene in age and composed mainly of agglomerates (andesitic in fine-grained tuff) and streamdeposited conglomerates (an agglomerate is composed of angular volcanic ejecta, in contrast to conglomerate particles rounded by stream transport). The Panama Formation outcrops are rapidly being altered, especially near the former Canal Zone, because these local hilltop deposits are extensively removed for valley fill and road construction.

The Gatuncillo sediments consist of mudstones, siltstones, quartz sandstone, impure ben-

THE CULEBRA FORMATION

The Culebra Formation (Hill, 1898) takes its name from a town located in the central Gaillard Cut during the construction period. The formation outcrops in very limited areas on either side of the Canal along the Gaillard Cut (Fig. 2). Stratigraphic relations are exceedingly complex because of extensive faulting in the area. In a distance of ca. 3 km, more than 113 faults have been observed along Las Cascadas Reach to the north. In one section adjacent to the Canal, along Las Cascadas, Empire, and Culebra Reaches, lefthanded fault motions represented in a distance of 4 km total 4 km of displacement. The Culebra Formation lies unconformably on the Gatuncillo Formation, and has a thickness of about 165 m. It is overlain by the Las Cascadas Formation as revealed by a core (SC-108) drilled at the Las Cascadas Reach (9°04'N, 79°41'W; Canal Station 1615). The Culebra is composed mainly of calcareous sandstones and siltstones, with interbedded lenses of coalified lignite and carbonaceous shales. Like the Gatuncillo Formation, the Culebra also represents a nearshore, transgressive depositional environment and specifically an estuary deposit as evidenced by the very thinly bedded, dark, fine-grained sediments, some of which contain fragments of land plants. In the older literature reference is made to the Empire or Emperador limestone member of the Culebra Formation. This "massive, creamcolored coralliferous limestone, formally exposed in shallow quarries at Empire, was named the Empire limestone by Hill (1898: 195-196). Empire, now abandoned, was a village on the original line of the Panama Railroad near Culebra and about half a mile west of Gaillard Cut"

tonite, and coralline and foraminiferal limestone. Interbedded are lenses of lignite ranging from a few centimeters to 1-2 m in thickness. Locally there are overlying deposits of marine limestone. The sequence is typical of nearshore deposition in tropical environments, since lignites presently form under such conditions (Cohen & Spackman, 1972; Scholl, 1964a, 1964b), and those in the Gatuncillo sediments contain Rhizophora pollen. The corals fringing the volcanic islands that occupied the region of present-day central Panama during the Eocene, and contributing to the coralline component of the Gatuncillo Formation, further reflect tropical depositional environments. Surrounding most of the Gatuncillo Formation to the east, north, and west are extensive areas mapped as pre-Tertiary. These include altered basaltic and andesitic lavas and tuff, and other dioritic and dacitic intrusives. Woodring (1957-1982) has made extensive studies on the Tertiary mollusks from the Canal Zone. From the Gatuncillo Formation he reports a fauna most similar to those elsewhere of middle to late Eocene age. Cole (1952) studied the larger foraminifera of the Gatuncillo Formation. He reported 21 species, 18 of which are recorded elsewhere in the late Eocene. The remaining three



FIGURES 4, 5. Roadside exposure of the middle(?) to Late Eocene Gatuncillo Formation near Alcalde Díaz (9°7'N, 79°32'W; locality D), Republic of Panama (January 25, 1983). -4. General view showing basal lignite and overlying siltstone. -5. Close-up of lignite area shown in lower-left corner of Figure 4.



FIGURE 6. The southwest face of Gold Hill on the Gaillard Cut section of the Canal, Republic of Panama. Core material from the lower Miocene Culebra Formation was obtained from a well drilled in front of Gold Hill on the west side of the Canal (9°02'N, 79°38'W; drill site 1 on Fig. 1). The subsurface stratigraphy for the Culebra Formation at this site is summarized in Tables 1 and 2 from the well log data. The line separates an unnamed basalt of late Miocene or early Pliocene age (above) from upper lower Miocene agglomerates of the Pedro Miguel Formation (below).

(Woodring & Thompson, 1949: 237). The Emperador is now included as a member within the lower La Boca Formation.

Woodring (1957–1982) assigns the Culebra to the lower Miocene based on mollusk data. Stratigraphic relations with overlying fossiliferous deposits, and one tentative potassium-argon date from the Cucaracha Formation (see below), further suggest a lower Miocene age. In previous stratigraphic columns (e.g., Woodring & Thompson, 1949), the Culebra Formation was assigned to the upper Oligocene. A well was drilled through the Culebra Formation (locality 1 on Fig. 1) that provided fossiliferous samples and log data detailing the subsurface stratigraphy of the formation. The well was completed on January 8, 1958 and the field log was filed with the Engineering and Construction Bureau of the Panama Canal Commission. Subsequently the cores were discarded, but copies of the logs, unprocessed samples, vials of processed material, and slides are preserved in the palynology collections at Kent State University.

The samples were obtained from Hole No. GH-9; latitude $9^{\circ}02'N + 2912.3$, longitude $79^{\circ}38'W + 5561.5$; ground elevation 29.6 m (+96.1 ft.); core recovery 124 m (402.6 ft.; 80.5%) from a total section of 154 m (500.2 ft.); project— Gold Hill Investigation; location—in front of Gold Hill on the west side of the Canal and in front of the Model Slope which is just north of Contractor's Hill (Fig. 6). Fifty-seven samples were taken along the 124 m section (Table 1), primarily from carbonaceous layers within the predominantly sandstone section (labeled in our

collections as PAN Core, Culebra Formation). From these, 21 samples were processed and all contained fossil pollen and spores. The stratigraphy and lithology for portions of the core sampled are given in Table 2.

THE CUCARACHA FORMATION

The Cucaracha Formation outcrops on both sides of the Canal from Hodges Hill southward to the area of Pedro Miguel Locks. The most

TABLE 1. Samples from Panama Canal Company's Hole No. GH-9, Contractor's Hill locality, Culebra Formation (lower Miocene), Republic of Panama. Figures represent depth in feet along the core. Arrangement of the samples is subdivided according to core box sequence used by the PCC. Although these boxes and samples have been discarded, the sequence is still referred to in the summary section of the Geological Field Log of the Contractor's Hill locality, Gold Hill Investigation. The ash flow or ignimbrite is a layer of volcanic debris 8 m thick with tentative potassium-argon dates of 22.2 \pm 1.7 and 18.9 \pm 2.2 Ma (Wood-ring, 1982: 551).

The lower 0.5 m of the ash flow contains numerous carbonized logs, twigs, and roots. In places, the old stumps were found still upright with roots extending into the strata below. This zone represents an old forest layer that was carbonized and buried by an explosive volcanic eruption. Immediately to the north of the area, just north of Contractor's Hill at the Model Slope, 75% of the log bases exposed during Canal widening excavations pointed north and northeasterly indicating the direction from which the eruption came. The 100 m of strata below the ash flow consists primarily of alternating, recurrent layers of clay shale, tuffaceous siltstone, tuffaceous sandstone, and conglomerate with scattered layers of lignitic shale. This sequence is repeated many times throughout the lower part of the section. At the base of the section is a basal conglomerate containing abundant oysters, indicating a nearshore depositional environment. Occasional well-worn specimens of Miogypsina cushmani can be found in some of the upper layers of sandstone. These were likely derived from nearby outcrops of the Culebra Formation that had been uplifted by tectonic activity prior to the deposition of this part of the Cucaracha Formation. The dominant plant is a coarse grass, Saccharum spontaneum L., introduced from the Old World tropics and now widespread throughout the Canal area. On fresh exposures this grass initially aligns itself along the lignite outcrops (Fig. 8) and is a convenient marker for these organic-rich sediments. Later, as the grass spreads and slumping of the sediments occurs, this relationship is obscured.

Box 12 of 17			Box 15 of 17	Box 16 of 17	
370.2ª	392	424	446.7	474	
376.5ª	394.3	424.6	448ª	476	
377ª	407ª	425ª	449.4	479	
378.4ª	409	427.5	450	481	
382ª	411	428.6	451	482.5	
383	412.6	433.3	452ª	483.6	
385.7	415.5ª	435	454.6	486	
388.7		437.9ª	456ª	488ª	
		438.6	459.6	490.6ª	
		440.7	461ª	491ª	
		441.9	463.4ª	491.6ª	
		442.9ª	466	494	
		444.6	469.8ª	494.9	
			470.6ª	495.8	
				496.8	

* Samples from which fossil pollen and spores have been recovered.

prominent and accessible outcrops are on the southwestern side of the Cucaracha Reach sector of the Gaillard Cut between Canal Stationing 1983 and 2010. The formation is named after a railroad station and a small town that existed prior to Canal construction.

The Cucaracha Formation is composed mostly of bentonitic clay shales, tuffaceous siltstones, and sandstones with discontinuous lenses of lignite and freshwater conglomerates. The total thickness of the Cucaracha Formation is about 183 m. The formation is divided into an upper and a lower zone. A layer of ash flow or ignim-

Along road K-2 about 0.8 km northwest of the intersection with K-15 in the Gaillard Cut section of the Canal is a roadside exposure of the

brite divides the two zones.

The upper part consists of the following: clay shales over siltstone, an upper lignite bed ca. 0.5 m thick, a clay shale, a conglomerate ca. 0.5 m thick, a lower lignite bed ca. 0.5 m thick, a clay shale, and the ash flow at the base. The dip of the beds is 15°, and the dip of the slope is about 20°. The lignites range from a black, friable, fissile, lignite shale to a coalified lignite. All of these beds in the upper part are in fault contact with the basalt in the upper part of the hill. Cucaracha Formation (our locality C, samples 57a-66, Figs. 1, 2, 7, 8). Across the road on the Canal side the ash flow continues and the lower 1.5 m includes highly decomposed logs representing the forest layer at this site. Below the tuff is another clay shale, then a 0.7 m lignite near water level that is not evident on the roadside section. This lignite rests on a clay shale with 25 cm diameter siderite (FeCO₃) concretions.

At this locality there is a small utility building adjacent to a power pole (Fig. 7). About 4 m

D. 12 Dev 12 Dev 14 Dev 15 Dev 16

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TABLE 2. Stratigraphy and lithology of samples from the Culebra (lower Miocene) Formation, Republic of Panama. Representative data selected from Panama Canal Company's Geological Field Log, Hole No. GH-9, Contractor's Hill locality, Gold Hill Investigation.

Elevation	Depth	Descripton of Material	Core
(ft.)	(ft.)		Recovery
-270.2	366.3	SANDSTONE, RH 1–2, moderately soft to medium hard, moderate strength, moderate jointing, very thin bedding, medium to coarse grained, variably calcareous and carbonaceous, fossiliferous; color: mottled medium and dark grays. NOTE: thin, highly carbonaceous layers make innumerable dark gray lines.	26.9 (90.5%)

-299.9 396.0 SANDSTONE, RH 1-2, moderately soft to medium hard, moderate strength, moderate jointing, very thin bedding, medium to coarse grained, variably calcareous and carbonaceous, fossiliferous; color: mottled medium and dark grays. NOTE: thin, highly carbonaceous layers make innumerable dark gray lines.

49.4 (92.5%)

50.0

(98.4%)

493

- -353.3 449.4 SANDSTONE, RH 1-2, soft to medium hard, moderate strength, moderate jointing, very thin bedding; fine to medium grained with very high silt content; variably calcareous, carbonaceous, and fossiliferous; color: mottled medium and dark gray; thin carbonaceous layers make innumerable dark gray lines.
- -404.1 500.2 SANDSTONE, RH 1-2, soft to medium hard, moderate strength, moderate jointing, very thin bedding; fine to medium grained with very high silt content; variably calcareous, carbonaceous, and fossiliferous; color: mottled medium and dark gray; thin carbonaceous layers make innumerable dark gray lines. Bottom of hole.

above and to the left of the pole is a conspicuous conglomerate layer 1 m thick. The conglomerate terminates abruptly and continues on the other side of the pole about 4 m down in the section. This displacement is 9 m of left lateral motion, and the fault is one of the hundreds that characterize the Gaillard Cut section of the Canal. All samples were collected to the right of the fault line (facing the slope), and no faults were observed through the section sampled.

About 0.7 km further to the right (NW) is part of the locality from which Whitmore and Stewart (1965) reported fossil mammal bones, all belonging to a fauna with distinct northern affinities. The collecting sites of the mammal bones take into account the unusually large number of faults, frequently obscured by slumping and dense vegetation, that occur within very short distances.

A well was drilled near this site on October 4, 1958 (Hole No. PA-33; latitude $9^{\circ}01'N + 5914.9$, longitude $79^{\circ}38'W + 2300.0$; ground elevation 56 m (+182.7 ft.); core recovery 40.8 m (132.5 ft.; 71.4%); project—Cucaracha Reach Widening Studies; location—Cucaracha Reach). The drilling logs are filed with the Panama Canal Commission, and copies are in the palynology collections at Kent State University. Relevant portions of the log are summarized in Table 3. It is noted that only 71.4% of the core was re-

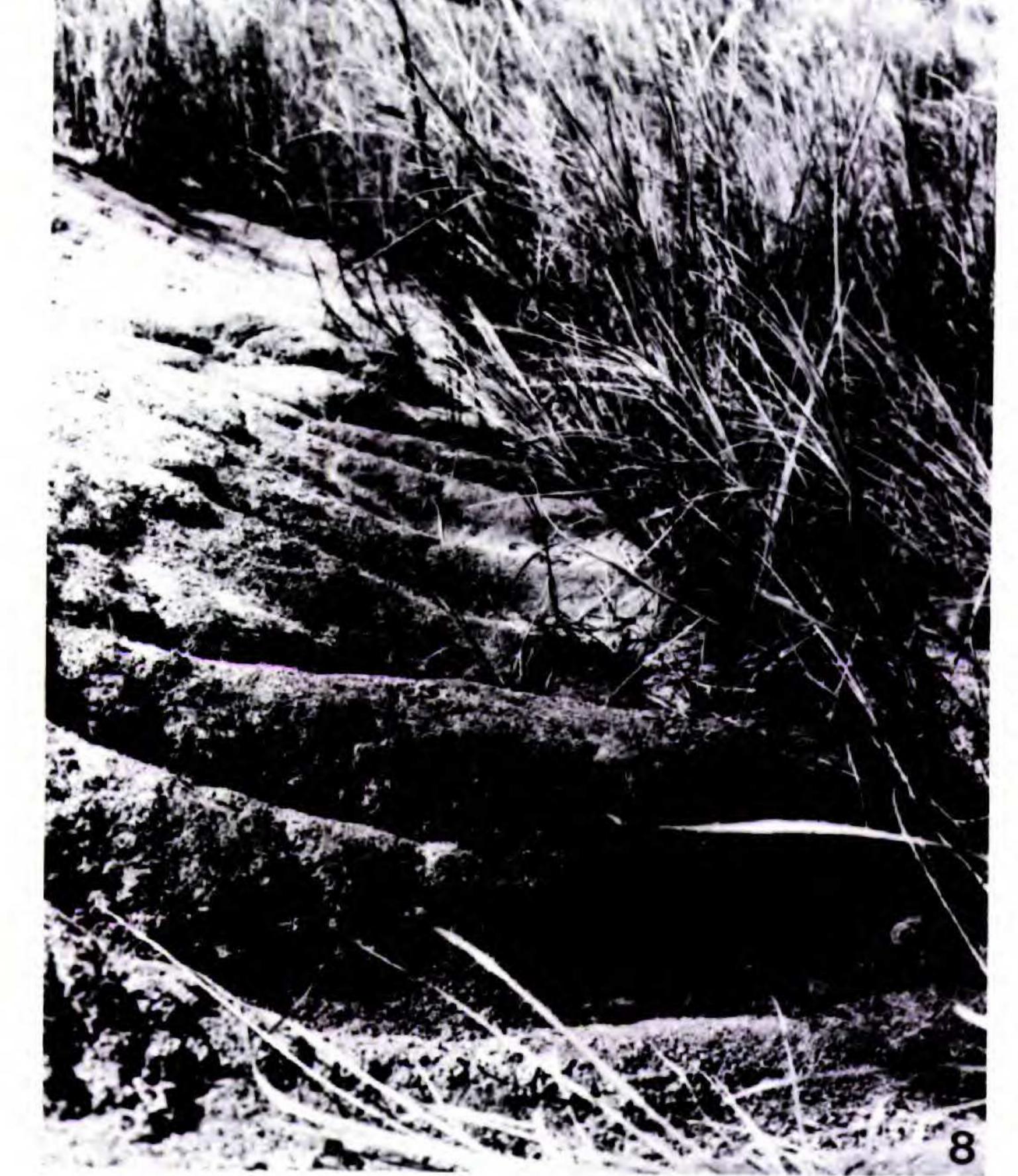
extended from Canal Station 1994 in the north to Canal Station 2011 in the south. This site also contains large numbers of presumably crocodilian coprolites. Several of these were collected and processed, but the palynomorphs were poorly preserved and in low concentrations. In this distance of ca. 0.7 km, two faults intervene, and, although the mammal beds are altitudinally equivalent to the layers sampled for fossil palynomorphs, they are stratigraphically lower. Clearly, sampling in this complex region must covered, and among the missing strata are the conglomerate layer and the lower roadside lignite described earlier. The initial lignite referred to in the log is the uppermost layer in the roadside section.

The general sedimentology of the section, and the sequence of lithologies, reveal the overall nature of the depositional environment. Lignites form under coastal, brackish water conditions where slow-flowing rivers empty onto a relatively broad coastal plain and where a dense vege494

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FIGURES 7, 8. Exposures of the Cucaracha Formation (locality C) along the banks of the Canal, Republic of Panama. -7. Alternating layers of dark lignites and lighter ash and conglomerates. -8. Lignite layer with 15-20 cm thick overburden of eroded ash and lignite. Note the horizontal alignment of the grass Saccharum spontaneum L. along the lignite zone.

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495

6.8

(53%)

19.2

(80%)

48.3

(37%)

2.0

(83%)

28.6

(93%)

Stratigraphy and lithology of samples from the Cucaracha (lower Miocene) Formation, Republic TABLE 3. of Panama. Representative data selected from Panama Canal Company's Geological Field Log, Hole No. PA-33, Cucaracha Reach locality.

Elevation	Depth	Description of Material	Core
(ft.)	(ft.)		Recovery
+111.2	71.5	LIGNITIC SHALE, RH-1, soft, weak, closely jointed, thin bed- ded; contains an abundance of carbonaceous plant debris; color: dark gray to black. (This is the uppermost lignite layer described from the roadside exposure from which fossil pol- len-bearing samples were collected.)	1.7 (100%)

+109.5	73.2	CLAY SHALE, RH-1, soft, weak, very closely jointed with joints highly slickensided; consists of a fine-grained, water-laid vol- canic tuff highly altered to montmorillonite and bentonitic clay minerals; color: medium gray-green. (Note that only 53% of the core was recovered; missing is the conglomerate and basal lignite layer described from the roadside section.)
+102.7	80.0	ASH FLOW, RH-3, hard, strong, moderate jointing, massive bedding, fine-grained, porphyritic, agglomeratic; consists of a dacitic ignimbrite; color: purple, greenish gray, and brown.
+85.0 (Canal wa	97.7 ater level)	(This is the layer from which the K-Ar date was obtained; the lower 2 feet represent the old forest layer.)
+78.7	104.0	CLAY SHALE, RH-1, soft, weak, very closely jointed and slick- ensided, thinly bedded; consists of a fine-grained volcanic tuff
+35.0	147.7	highly altered to montmorillonite and bentonitic clay min-
(Bottom	n of canal)	erals; silt content increases with depth; color: gray-green.
+30.4	152.3	LIGNITIC SHALE, RH-1, soft, weak, closely jointed, thinly

bedded, contains an abundance of carbonaceous plant debris; color: dark gray to black. (This is the layer on the Canal side of the road below the lowermost layer on the roadcut exposure.)

+28.0

CLAY SHALE, RH-1, soft, weak, very closely jointed and slickensided, thinly bedded; consists of a fine-grained volcanic tuff highly altered to montmorillonite and bentonitic clay minerals; variably silty and sandy; contains some calcareous concretions in upper portion; color: 157.4 to 165.6, gray-green, 165.6 to 172.9, gray-green mottled with red-brown, 172.9 to 184.4, red-brown, 184.4 to 185.6, gray-green mottled with red-brown. NOTE: Some scattered calcareous concretions in red-brown layer from 180.6 to 181.4 ft. depth (these are the siderite concretions discussed previously).

-2.9

Bottom of hole. 185.6

from land vegetation. Extensive volcanism is tation (frequently dominated by mangroves) and documented by the tuffs (water-lain volcanic ash) and the basalt that caps the section.

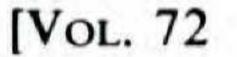
moderate off-shore currents allow organic detritus to accumulate. Climatic conditions under which modern lignites are presently forming are warm-temperate, subtropical to tropical (Cohen & Spackman, 1972; Scholl, 1964a, 1964b). The shoreline was periodically inundated, probably from local subsidence of the land rather than changes in sea level, as evidenced by the folding and faulting of the strata. The clays and silts contain both marine invertebrates and debris and limestones. The Emperador limestone is a

154.7

THE LA BOCA FORMATION

The La Boca Formation outcrops along both sides of the Canal from the Pacific entrance to Las Cascadas Reach. It is composed of mudstones, siltstones, sandstones, lignited shales, tuffs,





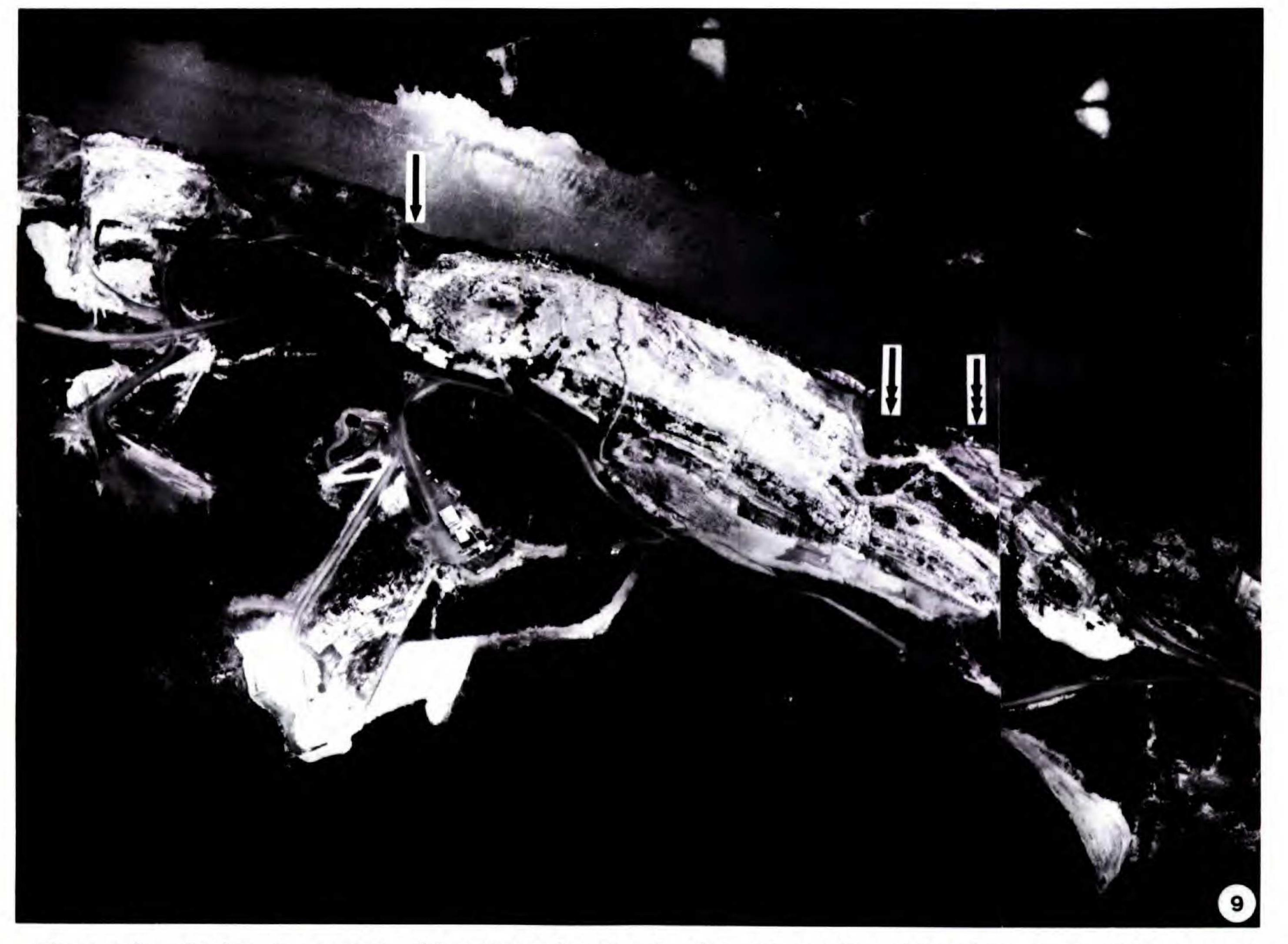
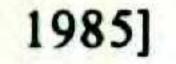


FIGURE 9. Aerial photograph of Las Cascadas Reach of the Canal, Republic of Panama, 1967, when this section was being widened from 90 m to 155 m. Single arrow designates collecting locality A in the early Miocene La Boca Formation at canal marker 1600 (1766 new system). Double arrow designates drilling site LBW-88 through the La Boca Formation at canal marker 1619 (1785 new system; 9°04'N, 79°40'W; log data summarized in Table 5). Triple arrow designates collecting locality B in the La Boca Formation at canal marker 1622 (1788 new system). Other samples were collected at markers 1625 (1791) and 1627 (1793) further to the right.

member of the lower part of the La Boca composed of coralliferous limestone reflecting warm, subtropical to tropical marine environments. These conditions are consistent with the layers of lignite that occur throughout the lower part of the section (see previous discussion, Cucaracha Formation). The sequence of sediments indicates a period of subsidence with bathyl siltstones (Blacut & Kleinpell, 1969) capping the section. The lignitic layers contain shells of marine invertebrates and substantial amounts of pyrite resulting from the oxidation of soluble ferrous compounds by iron bacteria. Woodring (1982) recognized 130 species of mollusks from the La Boca and their collective ranges suggest an early Miocene age.

marker 1600 (1766 new stationing), and locality B (samples 27-54) was at markers 1622 (1788), 1625 (1791), and 1627 (1793). At that time the Canal was being widened from 90 m to 155 m (Figs. 9–11), and by the January 1983 field season this construction was complete. Thus, compared to the present physiography, the 1967 samples were collected from strata 25 m up and 60 m out over the Canal. The beds dipped back into the slope 20–25° so that now the same lignite layers are nearly at water level and, in this area, near the La Boca-Las Cascadas contact (Fig. 12). In addition to these challenging alterations in the landscape, the Canal marking system has changed. Marker number 1625 (in our 1967 collections) is now 1791. This complicates any study dealing with the former Canal Zone and vicinity where canal markers were used as reference points. The Panama Canal Commission has a list correlating the new and old numbers, and

In September 1967, samples were collected from two Canal-side exposures of the La Boca Formation (Fig. 2). Our locality A (samples 1– 26) was on the Las Cascadas Reach at station



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FIGURES 10, 11. Exposures of the La Boca Formation at locality A, Las Cascadas Reach of the Canal, Republic of Panama, in 1967 during widening of the Canal [near canal marker 1600 (1766 new system); see Figure 9]. -10. General view of the locality. -11. La Boca Formation. Note the fault abruptly terminating the white tuff at the lower left of the exposure. Over 113 of these faults have been mapped in a distance of 3 km in the Gaillard Cut section of the Canal.

TABLE 4. List correlating the old collecting site numbers to the new collecting site numbers. From the Panama Canal Commission.

1967 Stationing	Present Stationing
1600	1766
1619	1785
1620	1786
1622	1788
1625	1791
1627	1793

On April 6, 1960, a well was completed at canal marker 1619 (old system; 1785 new stationing) near our collecting sites. The log provides general information on the stratigraphy and lithology of the La Boca Formation [Hole No. LBW-88; latitude $9^{\circ}04'N + 4586.4$, longitude 79°40'W + 4557.1; ground elevation 52.7 m (+171.4 ft.); core recovery 38 m (123.5 ft.; 72.0%); project-Canal Improvement; location-Las Cascadas Reach; old station 1619, 1785 new stationing]. The logs are filed with the Engineering and Construction Bureau of the Panama Canal Commission, and copies are in the palynology collections at Kent State University. The relevant portions of this log are summarized in Table 5. It is evident that the Culebra, Cucaracha, and La Boca Formations are similar in age (lower Miocene), and that stratigraphic relations are complicated by the highly faulted and altered nature of the sediments along the Gaillard Cut. Another source of earlier confusion resulted from an inadvertent coring error in the 1950s that led to incorrect correlations in some major paleon-

0.5

(16%)

25.9

(77%)

those pertaining to our collecting sites are summarized in Table 4.

It should also be noted that reference points may be cited on North American datum or Canal Zone datum. To change North American to Canal Zone datum, add 941 ft. to longitude and 942 ft. to latitude; to change Canal Zone to North American datum, substract 941 ft. from longitude and 942 ft. from latitude. Latitudes and longitudes cited in this study are on North American datum.

TABLE 5. Stratigraphy and lithology of samples from the La Boca (lower Miocene) Formation, Republic of Panama. Representative data selected from Panama Canal Company's Geological Field Log, Hole No. LBW-88, Las Cascadas Reach locality (station 1619).

Elevation (ft.)	Depth (ft.)	Description of Material	Core Recovery
+48.0 123.4	LIGNITIC SHALE, soft rock, closely jointed, joints slickensided, thin bed- ding; contains abundant carbonaceous plant debris and some marine bor- ings filled with fossiliferous material; color: dark gray to black.	1.5 (57%)	
+45.9	126.0	SILTSTONE, soft rock, thin bedding, moderate jointing with joints slick- ensided, fossiliferous at base; color: medium gray-green.	3.5 (77%)
+40.9	130.5	LIGNITIC SHALE, soft rock, closely jointed, joints slickensided, thin bed- ding; contains abundant carbonaceous plant debris and some marine bor- ings filled with fossiliferous material; color: dark gray to black.	0.0 (0%)
+38.4	133.0	SILTSTONE, soft rock, thin bedding, moderate jointing with joints slick- ensided, fossiliferous at base; color: medium gray-green.	0.9 (45%)

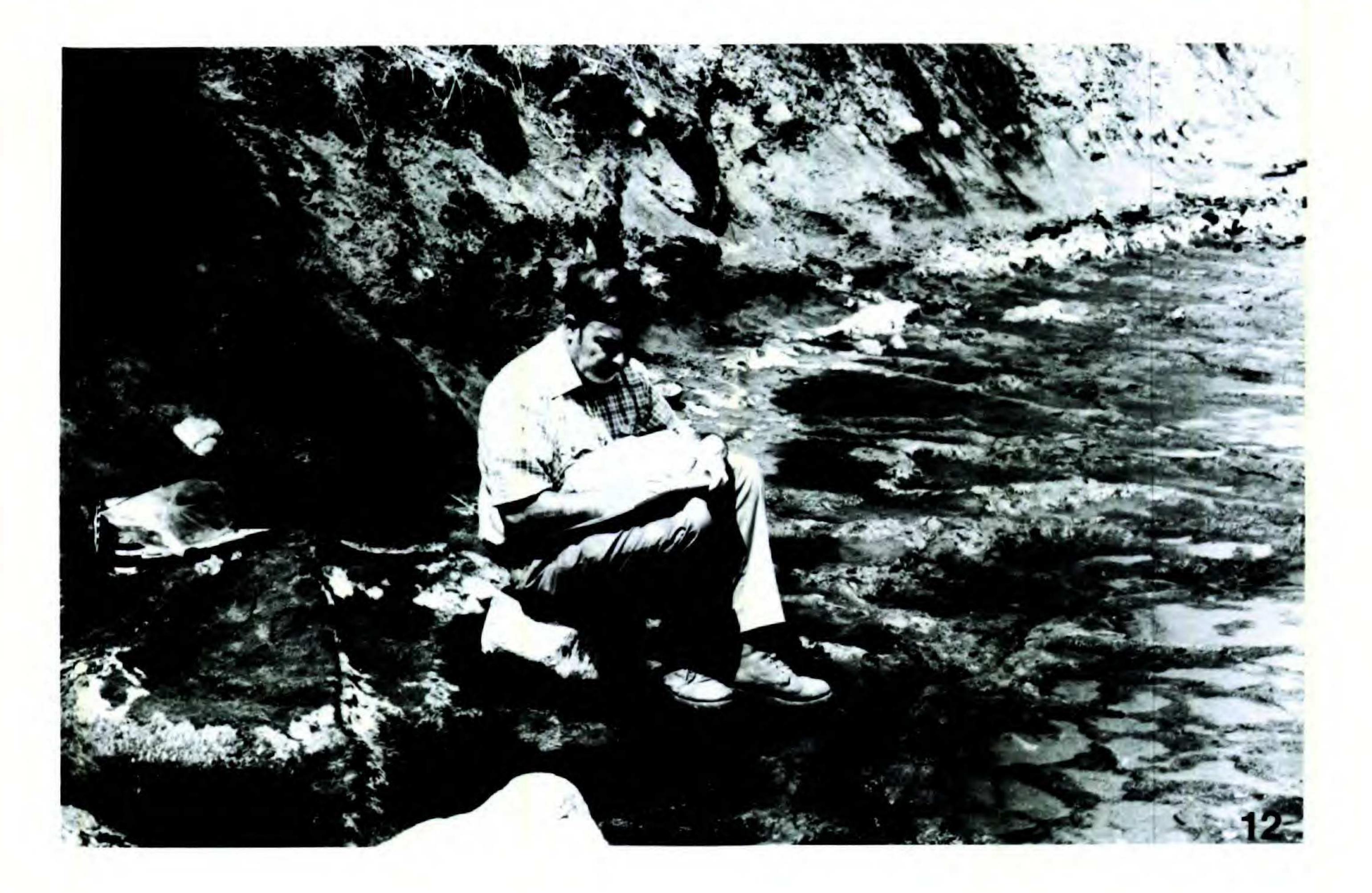
+36.4 135.0 LIGNITIC SHALE, soft rock, closely jointed, joints slickensided, thin bedding; contains abundant carbonaceous plant debris and some marine borings filled with fossiliferous material; color: dark gray to black.

+33.4 138.0 AGGLOMERATE, tuffaceous, soft rock, moderate jointing with joints open; some joints recemented with calcite and zeolite; massive bedding; consists of andesitic and basaltic pebbles and cobbles in a fine-grained, tuffaceous matrix of similar composition; some fragments are pumaceous; somewhat altered to various clay minerals and chlorite; material checks rapidly on exposure to air and falls apart; color: mottled grays and light greens. NOTE: Very tuffaceous in lower 11.0 ft., almost a tuff.

-0.1 171.5 Bottom of hole.

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FIGURES 12, 13. 12. New exposures of lower Miocene La Boca lignites (January 1983), Republic of Panama, after 61.5 m widening project started in 1967 was completed (see Figs. 9–11). This is locality B, and when samples were collected in 1967 the slope face was 25 m up and 60 m out over the Canal. Since the beds dip back at an angle of ca. 20–25°, the lignite bed (base of the figure) is now at water level. –13. Contact between the La Boca (marine phase) to the left (south) of the figure (R. S. Stewart) and the Las Cascadas (terrestrial volcanic) to the right (north; January 1983). La Boca is documented younger than Las Cascadas because it is on top, even though beds are vertical through uplift and left-lateral faulting. Slumping has obscured lithological differences between the formations at the contact (canal marker 1909).

TABLE 6. Location of pollen-bearing samples from the upper Miocene and Pliocene Gatun Formation and other Cenozoic deposits, Republic of Panama. Cores are designated by the Panama Canal Commission's system, and samples from each core are listed according to depth in feet (except HU's SL-60 sample at 40 ft. which is at a depth of ca. 127 ft.). Samples were collected in December 1962, by Elso Barghoorn and Alexandra Bartlett (HU), or in December 1963, by A. G. (KSU). All slides are presently in the palynology collections at KSU.

tological publications dealing with the Culebra and La Boca Formations. Van den Bold (1972, 1973) correlated the La Boca with the Culebra based on ostracod data and similarities in lithology. The same correlation was made by Woodring (1957) from mollusk evidence. R. H. Stewart (pers. comm.) found field evidence that was inconsistent with this correlation (see below) and re-examined the core from which the invertebrate fossils had been obtained. Stewart discovered that a piece of Cucaracha material from previous drillings had stuck in the core barrel and worked loose in the next drilling which was through the La Boca. Woodring (1982) subsequently corrected the error for the mollusk studles. Field stratigraphy reveals that the three formations are sequential within the early Miocene from the Culebra (oldest) through the Cucaracha, to the La Boca (youngest). This stratigraphy, used on the most recent version of the geologic map of Panama (Stewart et al., 1980), is based on the observation that in local areas the Cucaracha Formation sits on top of the Culebra. Above the Cucaracha is another formation, the Pedro Miguel. The terrestrial phase of the La Boca has not been observed directly on the Cucaracha, but it does interfinger with the Pedro Miguel, and therefore must be younger than the Cucaracha. In addition, the marine phase of the La Boca does rest directly on the Las Cascadas Formation (Fig. 13) which is the same radiometric age as the Cucaracha Formation. Thus, the Culebra, Cucaracha, and La Boca Formations, as presently understood, represent a time-stratigraphic sequence for the early Miocene in central Pan-

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Core SL-48 (Latitude 9°11' + 1331;
Longitude 79°55' + 4501)
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KSU	HU	
157		Gatuncillo
158		
162	162	

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Core SL-49 (Latitude 9°08' + 4113;
Longitude 79°57' + 1987)
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KSU	HU	
222.5		Gatun
223		
223.5		

Core SL-60 (Latitude 9°11' + 6042; Longitude 79°52' + 411) KSU HU

	40	Caimito Formation
Core SL-103 (Longitude 7	Latitude 9°16 9°52' + 2963	
KSU	HU	
	178	Quaternary
	250	Gatun
	253	
255.5		
257		

TABLE 7. Summary of log data for four cores through Tertiary and Quaternary formations in Panama from which fossil pollen and spores were recovered. Depth and elevation are in feet. See Table 6, Figure 1 (locality 2), and text for location of drilling sites.

Core	Elevation	Depth	Description of Material	
SL-48	+86.5	+86.5	0.0	Water
	+6.5	80.0	Overburden	
	-64.9	151.4	Top of weathered rock (samples SL-48, 157, 158, 162) SILTSTONE, medium hard to hard (OH 3-4); slightly to medium plastic; medium tough to tough; medium to high dry strength; clayey with streaks weathered to clay; slightly sandy, with very fine sand; color: mottled, gray	
	-76.6	163.1	and brown. (Gatuncillo Formation.) Recovery 10.4 ft. Top of sound rock SILTSTONE, medium hard (RH-2); massively jointed, no joints apparent; core in 0.1 ft. and smaller pieces broken during drilling by dry blocking;	

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TABLE 7. Continued.

Core	Elevation	Depth	Description of Material
			slightly sandy with fine sand; fairly clayey and marly; massively bedded, no bedding apparent; color: dark gray to gray. (Gatuncillo Formation.) Recovery 1.2 ft.
	-77.8	164.3	Final depth
SL-49	+86.9	0.0	Water
	+14.9	72.0	Overburden
	-133.2	220.1	Top of sound rock (samples SL-49, 222.5, 223, 223.5)

501

SILTSTONE, soft to medium hard (RH 1-2); massively jointed, no joints apparent; core in one piece 4.6 ft. long and in 0.1 ft. and smaller pieces, broken during drilling by dry blocking; slightly sandy with fine sand; fairly clayey; quite marly with scattered white streaks of shell fragments; massively bedded, no bedding apparent; friable; color: dark gray. (Gatun Formation.) Recovery 4.7 ft.

- -138.9 225.8 Final depth
- +87 0.0 Water
 - +6 81.0 Overburden

SILT, CLAY, AND ORGANIC MATERIAL, laid down since formation of Gatun Lake.

- -1.0 88.0 GRAVEL AND SILT.
- -4.7 91.7 SILT AND CLAY, soft to medium soft (OH 1-2); loose; medium plastic; slightly spongy at plastic limit, friable below plastic limit; very weak; low dry strength; sticky, high water content, and containing many carbonaceous wood fragments; color: dark gray and black. (Atlantic Muck.) Recovery 32.2 ft.
- Top of weathered rock (sample SL-60, 40) 127.3 -40.3SANDSTONE, medium hard to very hard (OH 3-5); jointing apparent at base only; silty; bedding not apparent; color: gray-green and brown. (Weathered Caimito Formation.) Recovery 9.8 ft. Top of sound rock 147.0 -60.0SANDSTONE, medium hard to hard (RH 2-3); closely jointed; core recovered in poor condition in 0.01-0.4 ft. lengths with 0.1 ft. lengths and fragments predominant; medium grained, silty, with occasional calcareous lenses near the base; bedding where apparent inclined about 5°; color: light gray-green with calcareous lenses almost white. (Caimito Formation.) Recovery 6.18 ft. Final depth 186.3 -99.3

SL-60

SL-103

- +85.7 0.0 Water
 - +47.7 38.0 Fill
 - +17.4 68.3 Overburden (sample SL-103, 178)
- -163.3 249.0 Top of weathered rock (samples SL-103, 250, 253) SANDSTONE, hard (OH-5 to RH-1), silty; locally clayey; scattered streaks of light blue-gray clay; slightly waxy locally; checks upon drying; color:
 - dark gray; grades into underlying sound rock. (Weathered Gatun Formation.)
- 168.4 254.1 Top of sound rock (samples SL-103, 255.5, 257)
 SANDSTONE, soft to medium hard (RH 1-2); massively jointed; medium grained; silty; carbonaceous; fossiliferous; contains scattered small pyrite grains; dark gray and greenish gray; core recovered in 0.5-2 ft. lengths. (Gatun Formation.) Recovery 10 ft.

-178.4 264.1 Final depth

ama. These strata provide a rare opportunity in tropical paleobotany to study the vegetational history of a single region through a defined segment of Tertiary time.

THE GATUN FORMATION

The Gatun Formation was named by Howe (1907: 113–114) from the type region extending from the bluff overlooking Gatun Lake near Gatun, northward to Mount Hope, formerly known as Monkey Hill, near Colon (Woodring & Thompson, 1949). Surface outcrops are extensive on the north (Caribbean) side of the Canal bordering the northern shore of Lake Gatun. The rocks are sandstone, siltstone, tuff, and conglomerates typical of nearshore deposition. The Gatun Formation is relatively unfaulted, whereas the nearby Eocene, Oligocene, and lower Miocene formations are heavily faulted. Thus, the stratigraphic position and geomorphology indicate a post lower Miocene age, although the Gatun Formation has not been observed in the field to rest directly on any of these. The Gatun Formation does rest with a strong, angular unconformity on the pre-Tertiary, Cretaceous volcanics and sediments. There are ash flows or pumice

of our studies, we are now tentatively accepting the younger age assignment.

In 1962 the Panama Canal Commission drilled a series of wells in Gatun Lake to test the foundation for new water storage construction as part of the Trinidad Dam studies. The upper portions of these cores penetrated pollen-bearing post-glacial sediments and were used by Bartlett and Barghoorn (1973) for their study of Quaternary vegetational history and sea-level changes in Panama. The lower portions of the cores that penetrated surface Gatun Formation sediments also contained a rich pollen and spore flora. It is fortunate that samples from the cores were obtained because all surface exposures are marine and none are known to contain plant microfossils. Samples containing fossil pollen and spores are listed in Table 6, and the location of the drilling site is indicated as locality 2 on Figure 1. Relevant log data from the cores are summarized in Table 7.

In the preceding sections the age, stratigraphic relationships, lithology, and depositional environments are summarized for five pollen/ spore-bearing Tertiary formations in Panama. Attention is devoted to the original location of collecting sites; alteration in the landscape that has affected these formations; noting changes in the Canal marking system and datum reference points that can confuse comparison with previously published studies; noting errors in earlier correlations; and recording the permanent location of unpublished well logs, samples, processed material, and slides in the palynology collections at Kent State University. The rationale for providing these details in an introductory paper is three-fold. First, it is convenient to integrate geological information on the several formations in a single publication. Second, it is possible that these lignite beds will be further altered or destroyed through construction activities along the Canal, or rendered no longer accessible because of political changes affecting Central America. For example, the core material used by Bartlett and Barghoorn (1973) for their study of Quaternary vegetational history in Panama, previously housed in storage facilities of the Panama Canal Commission, has been destroyed. The Tertiary portions of these cores, including all core material mentioned in this paper, measuring hundreds of thousands of feet and containing vast amounts of irretrievable information on the biology and geology of Panama,

beds within the Gatun sediments that may eventually provide radiometric dates.

The upper part of the Gatun Formation is distinctly marine. Foraminifera from offshore, presumed Gatun sediments (DSDP, R. H. Stewart, pers. comm.), contain some Pliocene species, and Vokes (1983) believes, on the basis of other invertebrates, that the Gatun could be as young as basal Pliocene. Near the Refineria Panama, Colon, a small knoll is composed almost exclusively of shells of marine invertebrates, especially Turitella. Woodring (1957-1982) has made extensive studies of mollusks from this and other Gatun localities, and these provide another basis for estimating the age of the formation. A total of 339 species have been described, and collectively they were interpreted to suggest a middle Miocene age. This assignment is used on the most recent version of the geologic map of Panama (Stewart et al., 1980). More recently, however, R. H. Stewart (pers. comm.) believes that a reassessment of the paleontological evidence, combined with observations on the stratigraphy, suggests that the Gatun Formation may be upper Miocene and Pliocene in age. A preliminary survey of the pollen and spores reveals an assemblage quite modern in aspect, and, for purposes

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were also discarded. Fortunately, samples were obtained in 1964 and 1967, and these constitute a major part of the present study. Finally, individuals now in residence in Panama (R. H. Stewart and J. L. Stewart) and other life-long students of Central American paleontology (e.g., W. P. Woodring) will soon be altering these direct associations with Panama. Their cooperation in facilitating almost every recent paleontological investigation within the Canal Zone is widely recognized, together with their impressive knowledge of local field geology and the extensive unpublished literature. Consequently, it seems timely to initiate these studies on the Tertiary history of vegetation in Panama with a revised summary of the geology of the formations.

GRAHAM, ALAN. 1976. Studies in neotropical paleobotany. II. The Miocene communities of Veracruz, Mexico. Ann. Missouri Bot. Gard. 63: 787-842.

— & D. M. JARZEN. 1969. Studies in neotropical paleobotany I. The Oligocene communities of Puerto Rico. Ann. Missouri Bot. Gard. 56: 308– 357.

HILL, R. T. 1898. The geological history of the Isthmus of Panama and portions of Costa Rica. Bull. Mus. Comp. Zool., Harvard Coll. 28: 151-285.
HOWARD, R. A. 1973. The vegetation of the Antilles. Pp. 1-38 in A. Graham (editor), Vegetation and

LITERATURE CITED

- BARTLETT, A. S. & E. S. BARGHOORN. 1973. Phytogeographic history of the Isthmus of Panama during the past 12,000 years (a history of vegetation, climate, and sea-level change). Pp. 203–299 in A. Graham (editor), Vegetation and Vegetational History of Northern Latin America. Elsevier Publ. Co., Amsterdam.
- BLACUT, G. & R. M. KLEINPELL. 1969. A stratigraphic sequence of benthonic smaller foraminifera from the La Boca Formation, Panama Canal Zone.

- Vegetational History of Northern Latin America. Elsevier Publ. Co., Amsterdam.
- Howe, E. 1907. Report on the geology of the Canal Zone. Annual Rep. Isthmian Canal Comm. 1907: 108-138.
- RAVEN, P. H. & D. I. AXELROD. 1974. Angiosperm biogeography and past continental movements. Ann. Missouri Bot. Gard. 61: 539-673.
- SCHOLL, D. W. 1964a. Recent sedimentary record in mangrove swamps and rise in sea level over the southwestern coast of Florida, Part I. Marine Geol. 1: 344-366.
 - ——. 1964b. Recent sedimentary record in mangrove swamps and rise in sea level over the southwestern coast of Florida, Part II. Marine Geol. 2: 343-364.
- STEWART, R. H. & J. L. STEWART (with the collaboration of W. P. Woodring). 1980. Geologic Map of the Panama Canal and Vicinity, Republic of Panama. Scale: 1:100,000. U.S. Geol. Surv. Misc.

Contr. Cushman Found. Foram. Res. 20: 1-22. COHEN, A. D. & W. SPACKMAN. 1972. Methods in peat petrology and their application to reconstruction of paleoenvironments. Bull. Geol. Soc. Amer. 83: 129-142.

COLE, W. S. 1952. Eocene and Oligocene larger foraminifera from the Panama Canal Zone and vicinity. Profess. Pap. U.S. Geol. Surv. 244: 1-41.
 CONEY, P. J. 1982 [1983]. Plate tectonic constraints

on the biogeography of Middle America and the Caribbean region. Ann. Missouri Bot. Gard. 69: 432-443.

- CROAT, T. B. 1978. Flora of Barro Colorado Island. Stanford Univ. Press, Stanford.
- GENTRY, A. H. 1982 [1983]. Neotropical floristic diversity: phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny? Ann. Missouri Bot. Gard. 69: 557-593.
 GOMEZ-POMPA, A. 1973. Ecology of the vegetation

Invest. Map I-1232 (map also included in Woodring, 1982).

VAN DEN BOLD, W. A. 1972. Ostracoda of the La Boca Formation, Panama Canal Zone. Micropaleontology 18: 410-442.

——. 1973. La posición estratigráfica de la formación La Boca, Panama, Zona del Canal. Publ. Geol. ICAITI 4: 167–170.

VOKES, E. H. 1983. Additions to the Typhinae (Gastropoda: Muricidae) of the Gatun Formation, Panama. Tulane Stud. Geol. Paleontol. 17: 123–134.
WHITMORE, F. C. & R. H. STEWART. 1965. Miocene mammals and Central American seaways. Science 148: 180–185.

WOODRING, W. P. 1957-1982. Geology and paleontology of Canal Zone and adjoining parts of Panama. Profess. Pap. U.S. Geol. Surv. 306A-F.

— & T. F. THOMPSON. 1949. Tertiary formations of Panama Canal Zone and adjoining parts of Panama. Bull. Amer. Assoc. Petrol. Geol. 33: 223–247.

of Veracruz. Pp. 73–148 in A. Graham (editor), Vegetation and Vegetational History of Northern Latin America. Elsevier Publ. Co., Amsterdam.